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SOMATIC CHROMOSOMES IN TRADESCANTIA

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INTRODUCTION

In 1913 the writer published the results of a study of chromosome behavior in the somatic cells of *Vicia faba*, the principal conclusion reached being that the splitting of the chromosomes is a phenomenon of the prophase. This view was directly opposed to that of Lundegårdh (1910, 1912), Fraser and Snell (1911), and Miss Digby (1910), who had contended that the telophasic alveolation of the chromosomes represents a splitting, and that the chromosomes remain through the ensuing resting stages as double structures. It was pointed out by the writer that this latter interpretation is rendered untenable by two lines of evidence which appear when the various transformations of the chromatin are minutely examined: first, the telophasic alveolation is very irregular and transforms each chromosome into an alveolar and then into a reticular structure which is in no true sense double, although chance arrangement of the vacuoles may often make it appear so; and second, the reticular chromosome, after separating from its fellows in the common reticulum during prophase, gives rise in a peculiar manner to a single (*i.e.*, not double) slender thread in which vacuoles, all or nearly all of them new, appear and develop into the true split.

The theory of telophasic splitting has been restated by Fraser (1914), Digby (1914, 1919), and Nothnagel (1916), who have employed it in the attempt to solve the problem of the heterotypic prophase. This point is one of fundamental importance, and will be taken up in some detail in the discussion.

The present study of the somatic chromosomes of *Tradescantia virginiana* L. was undertaken not only to test the writer's position with respect to the time of chromosome splitting in somatic mitosis, but also, by determining more precisely the nature of the transformation of the chromosomes in the somatic telophase, to ascertain to what extent, if at all, this transformation will aid in the interpretation of the heterotypic prophase. Essentially the same methods were employed as in the former investigation of Vicia. Although the behavior of the chromatin in the two cases is strikingly similar, Tradescantia, so far as could be judged from the preparations obtained, proved to be inferior to Vicia for a study of the late prophases; for the analysis of the critical stages of the telophase and early prophase, however, it turned out to be quite superior, many exceptionally clear figures being obtained. Root tips alone were used.

Among previous works dealing with Tradescantia may be mentioned those of Strasburger (1900), Miyake (1905), and Farmer and Shove (1905). The first two papers treat of the maturation mitoses. Both Strasburger, in his figures 97–100, and Miyake, in his figures 152 and 153, suggest a process of alveolation in the chromosomes during the heterotypic telophase. Farmer and Shove give an account of both the somatic and the maturation mitoses. They speak of a "vesiculation" of the chromosomes in the somatic telophase, the chromatin becoming a "cloud of fine granules through the linin band"; and describe "broad band-like areas" with the chromatin in a dense "granular aggregation" during the early telophase. These conditions are faintly suggested in their figures 2, *2a*, 20, and 21. But in none of these investigations have the changes undergone by the chromatin been followed closely enough to afford evidence on the time of chromosome splitting, or on the precise manner of the transformation of the chromosomes into the resting reticulum and of the latter into chromosomes.

DESCRIPTION

In order to give an uninterrupted account of the history of the chromatin through the critical stages—the telophasic transformation of the chromosomes into the resting reticulum and the subsequent condensation of the latter into chromosomes—the description will begin with the metaphase.

Metaphase and anaphase. As is usually the case with long chromosomes, those of Tradescantia are inserted on the spindle by their middle points. Six of them are thus shown in figure 1 (a portion of the chromosome on the right has been cut away). Since no detailed comparison of all the chromosomes of the group has been made, it is not known whether or not this mode of insertion is an invariable one. The free ends of the chromosomes extend out in various directions, but most commonly lie more or less parallel to the axis of the mitotic figure. As Farmer and Shove also observe, the doubleness of the chromosomes reaches its maximum distinctness at this time.

Because of their mode of attachment to the spindle, the chromosomes take the form of V's as they move toward the poles at anaphase (figs. 2, 3). The mottled appearance shown by the chromosomes appears to be due very largely to their uneven contour, though unequal density of the chromatin in various portions of the chromosome may be partly responsible. Nothing which can be called internal granules or chromomeres has been distinguished at this stage, and only occasionally do any vacuoles make their appearance so early. As they reach the poles the chromosomes become much shortened and thickened, and contract into two dense groups in which the limits of the chromosomes can be made out only with considerable difficulty. The new cell plate now begins to be differentiated on the fibers between the two groups.

Telophase. After remaining in close contact for a short time the chromosomes begin to separate from one another, and as they do so they cohere at various points where their substance becomes drawn out to form anastomoses (fig. 5). Although it is possible that some of the anastomoses, which become very numerous in later stages, may originate after the manner of pseudopodia, it is clear that the earlier ones must be formed mainly by the coherence of the viscid substance of neighboring chromosomes originally in contact. Meanwhile the karyolymph has begun to form, the nuclear membrane differentiating where it comes in contact with the cytoplasm.

The telophasic alveolation or vacuolation of the chromosomes begins at about the time the latter begin to separate as above described. The vacuoles first appear within the chromosomes as somewhat obscure though rather sharply limited regions of circular or oval form (fig. 5). They develop not only along the axis of the chromosome but also near or against its periphery; in fact, an inspection of the figures shows that they may occur in almost every conceivable position and with no regular arrangement with respect to each other. At a slightly later stage they become clearer and more numerous (fig. 6).

This variety and irregularity in the arrangement of the vacuoles calls for special emphasis, because of the fact that the writers named in the first paragraph of this paper have interpreted the telophasic alveolation as a splitting, the chromosomes from this stage onward being consequently regarded as double. Attention is therefore directed to the conditions illustrated in figures 6–9. It is noticeable that the vacuoles may nearly all be along the margin of the chromosome (right edge of upper nucleus in figure 6), and also that two or three may lie side by side across the width of the chromosome (left edge of same nucleus). In figure 7 are shown two chromosomes in which the latter condition is especially pronounced; here it is manifestly impossible to speak of a split. Transverse sections of the chromosomes at these stages are particularly instructive (fig. 9). Such a section passing through a region where there is but one large vacuole more or less centrally placed has an appearance represented in figure 9*a*. A chromosome with a series of such central vacuoles would appear double if viewed from the side. This, however, is only a special case of a more general condition. Figures 9*b*–9*f* show sections passing through regions occupied by several vacuoles side by side, as in the chromosomes of figure 7 and those at the left in figure 6. It would seem to require no further argument to show that the chromosomes during these and the later telophase stages are not split ribbons or threads, but are irregularly alveolated cylinders; and that they can no more be called "double" than triple or quadruple.

The above described changes continue, gradually transforming the alveolated chromosomes with their anastomoses into a common reticulum. An examination of figures 10–13 will serve better than a written description to make clear the manner in which this transformation is accomplished. The whole nucleus enlarges, nucleoli appear, the anastomoses lengthen and apparently become more numerous, and the alveolation of the chromosomes becomes more complete (fig. 10). The chromosomes at this time usually show a distinct polarity in their arrangement, as represented semidiagrammatically in figure 8. As the vacuoles within the chromosome increase in size and number, their boundaries at the margin of the chromosome break down, allowing them to become continuous with the nuclear cavity. In this way the alveolar or vacuolate condition passes into a reticular one; each chromosome becomes an irregular netlike structure which is in no sense double. All of them together, with their connecting anastomoses, constitute the common reticulum of the late telophase and interphase or resting stages. The limits of the constituent chromosomes remain visible until a comparatively late stage (fig. 11).

Interphase and Rest. The degree to which the telophasic transformation is carried varies considerably in different nuclei, the amount of change being correlated with the rapidity with which the mitoses succeed one another. In the most active part of the root meristem it seems evident that the transformation may go no further than the stage represented in figure 11, the prophasic changes of the next mitosis setting in at once. In such an event the chromatin passes directly from the stage of figure 11 (telophase) to that of figure 14 (prophase): the anastomoses connecting the reticulate chromosomes begin to break down while the chromosomes are yet distinguishable, so that there is no time between the successive mitoses at which the limits of the chromosomes cannot be seen. It is plain that in such cases the structural identity of the chromosomes is not lost during the interphase.

The interphase condition most commonly found in the root meristem is that shown in figure 12. Here the telophasic transformation has been carried much further; the anastomoses for the most part cannot be distinguished from the other fine strands of the reticulate chromosomes, and the limits of the chromosomes cannot be made out with any certainty. Here and there are lighter regions which probably represent boundaries between the constituent chromosomes, and if the prophasic changes were to begin at this time the reticulum would almost surely break down along these lines. The chromatin may apparently continue in this state for some time, so it may properly be said to be in the "resting" condition.

In older tissue, but only rarely in the root meristem, the telophasic changes continue until the nucleus has the structure shown in figure 13. The chromosomes, all visible traces of whose limits have now been lost, form a common chromatic reticulum of very fine texture. Such a reticulum is ordinarily described as being made up of "granules of chromatin carried on a supporting network," and so it surely appears if not sharply stained or if viewed through lenses of insufficient resolving power. But careful examination, together with a comparison of the successive stages of the telophase, lead to a different interpretation. Since the structure of the fine reticulum is the direct outgrowth of the progressive transformation shown in figures 5–12, it seems more probable that the "chromatin granules" are merely the heavier portions of the alveolated and reticulate chromosomes, and that the lighter "supporting network" consists simply of the thinner portions of the same together with the delicate anastomoses. As pointed out in the case of Vicia, the finer strands stain much less deeply than the coarser portions, so that one easily gains the impression of separate chromatin granules connected by delicate threads of another material. But in a tapering strand the color grows gradually deeper in passing from the thinner to the thicker portion, a fact which indicates that the reticulum consists of but a single substance, or, more probably, that the chromatin substance is very fluid in consistency and free to diffuse about within the other material which composes the framework, as suggested by Grégoire (1906). Although much evidence which has been brought forward by various workers indicates the presence of two principal and morphologically distinct elements in the nuclear reticulum, it is nevertheless probably true that the above interpretation will apply to many accounts describing autonomous chromatin units on a supporting achromatic network.

Prophase. As the prophasic changes begin, the reticulum becomes somewhat coarser and commences to break up into irregular band-like portions (fig. 14). As pointed out in the preceding section, the telophasic changes in rapidly multiplying cells may go no further than the stage represented in figure 11, where the limits of the chromosomes can easily be made out. If, now, such a nucleus should enter upon the prophase, there can be little doubt that it would be along the lines of chromosome union that the reticulum would break down, since along these lines are the delicate anastomoses, which would be the first to give way as the band-like portions begin to condense. A reticulum in which the telophasic transformation has been carried further, as in figure 12, also breaks down along its lighter zones. From what has been seen in the case of figure 11, it seems evident that these zones for the most part represent the interchromosomal spaces, so that here also argument may be made for the structural continuity of the individual chromosomes through the interphase or resting stage. In the case of a nucleus with such a fine and uniform reticulum as that of figure 13, it is manifestly impossible to determine by direct observation whether or not the lines of prophasic separation coincide with those of the preceding telophasic union. The evidence for the structural individuality of the chromosomes must here be indirect, and such indirect evidence is afforded by the many known instances in which the chromosomes in successive mitoses, although lost to view during the resting stages, not only remain constant in number but maintain constant differences in size and shape. Additional evidence is found in the fact that in cells dividing repeatedly in one plane, as in the root meristem, the separate bands or chromosomes appear in the prophase with the same orientation as that shown by the chromosomes as they form the reticulum during the telophase (compare figs. 11 and 14).

The separating portions of the reticulum, each of them representing a chromosome, continue to condense, and the anastomoses between them become further broken down, so that they soon stand out with great distinctness (fig. 15). Since the early prophasic changes are in many respects simply the reverse of those occurring in the telophase, the structure of the chromosomes at these two stages is almost precisely the same. Vacuoles, or spaces enclosed during the condensation of the reticulum, may be found in all positions, median and peripheral, while large cavities open to the exterior on all sides. Transverse sections of chromosomes in this condition are shown in figure 16. It is perfectly evident that at this stage of the prophase, just as in the telophase, each chromosome is simply an irregular alveolar-reticulate cylinder, and has the form neither of a split thread or ribbon nor of a ladder-like structure characteristic of the incompletely split chromosomes of the later prophases. At the stage shown in figures 15 and 16 the chromosomes are in no sense double; the split marking the line of separation at the next metaphase has not yet appeared.

Each alveolar-reticulate chromosome now becomes transformed in a peculiar manner into a *single* (*i.e.*, not double) slender thread. Of all the morphological changes undergone by the chromosomes during mitosis this is one of the most difficult to observe and interpret. The staining must be particularly sharp to bring it out properly, and it is probable that it is passed through with considerable rapidity. These facts account in part for the absence of these stages from the descriptions of mitosis given by many investigators, and consequently for misinterpretations of the telophasic and early prophasic changes with respect to the splitting of the chromosomes. The transformation process, which is in progress in the nucleus shown in figure 17, is as follows.

As the chromatic material becomes increasingly condensed, the more slender strands, like the anastomoses at an earlier stage, and also the thinner walls bounding the peripherally situated enclosed spaces, become broken down, leaving the heavier portions of the chromosome in the form of a very irregular zigzag thread of uneven thickness. Various stages in this process are shown in figure 18. At the points marked *a* the dissolution of the finer portions can be seen occurring, and the reason for the crooked and lumpy appearance of the newly formed slender thread is apparent. In many cases the arrangement of the open spaces is such that the chromatic thread has a roughly spiral aspect, but in view of the relation it bears to the reticulate stages of the earlier prophases it can hardly be said to arise endogenously within the chromosome as some workers have maintained. The crooked thread at once begins to straighten out; this change in shape is associated with an equalization of the chromatic material, so that the thread gradually becomes more uniform in diameter. Here and there in the heaviest portions a few small vacuoles may for a time persist, but for considerable distances the thread is completely without them.

The true split now develops in the slender threads. Almost as soon as a portion of a thread becomes sufficiently equalized a number of new openings appear, and it seems highly probable that they are the outgrowth of small vacuoles which are formed anew along the axis of the thread. Some of the openings elongate a little, making the thread clearly double for short distances (fig. 19); here for the first time a portion of a chromosome can be said to be truly double. It is a matter of extreme difficulty—indeed it is probably impossible—to tell certainly whether these small vacuoles and openings are all new prophasic developments or are in part retentions from the resting stage and hence from the preceding telophase. Soon after their formation the slender threads, so far as can be determined with the best optical equipment, are certainly single and devoid of vacuoles for long distances, whereas the vacuoles become very numerous later. After a comparison of many chromosomes in these stages the writer has concluded that in all probability a vacuole or open space is now and then retained from an earlier stage, but that the great majority of vacuoles and spaces which develop into a split in the slender thread are formed anew in the prophase.

As the vacuoles increase in number and enlarge into openings extending through the thread, the latter shortens and thickens, and takes the form of an irregular ladder-like structure (figs. 20, 21). A nucleus in this stage (fig. 22) has a superficial resemblance to one in the early prophase stages (fig. 15), and some writers have confused them, omitting the important stages which intervene. In figure 15 the chromosomes are in the form of irregular alveolar-reticulate cylinders, as shown by their cross section (fig. 16), whereas in figure 22 they exist as thread- or ribbon-like structures partially split by a series of median openings and are clearly double in cross section (see the free and cut ends in figures 21–23).

As already stated, Tradescantia appears to be less favorable for a study of the later prophases than Vicia. The open spaces in the chromosomes do not run together to form a continuous split so early as in the latter plant. The material of some of the cross pieces connecting the sides of the partially split threads gradually flows to the two sides where it accumulates in the form of paired lumps simulating divided granules as fully described in the account of Vicia. Many of them, however, remain unchanged until a very late stage, so that even after the threads have become much shortened and thickened to form the conspicuous heavy spirem stages some of them may show the openings not yet developed into a complete split (figs. 22, 23). In other chromosomes the splitting process has gone further, making them almost completely double (at right in figs. 22 and 23). In nuclei of these stages it is not difficult to discover several free ends which are not due to the microtome knife, so that certainly at this time, and probably at earlier stages also, the chromosomes do not form a continuous spirem. On the other hand, it seems probable that some of the chromosomes may hang together end to end, since the number of ends which can be distinguished appears to be much smaller than the number which would be expected if all the chromosomes were free from one another.

The spindle now begins to differentiate in the cytoplasm, and the nuclear membrane contracts about the chromosomes. In the chromosomes the split now becomes complete, but as they continue to shorten and thicken their halves become so tightly pressed together that in many preparations they can scarcely be distinguished. As the contraction reaches its climax the nuclear membrane disappears (fig. 24), and the chromosomes, after loosening up as an irregular group, rapidly become arranged on the spindle with their halves clearly evident (fig. 1).

Discussion

A number of the features of somatic mitosis as the writer has found them have been compared with the results of other investigators in the paper on Vicia (1913) and need not be reconsidered here. In the present discussion attention will be limited to three important points: the time of chromosome splitting, the method of splitting, and the bearing of the results of this study on certain interpretations of the heterotypic prophase.

Time of chromosome splitting. Because of the exact manner in which the telophasic and prophasic changes are seen to occur when closely examined, the writer has contended that the definitive splitting of the chromosomes occurs in the prophase rather than in the telophase as several workers have urged. In the first place, the telophasic alveolation, as emphasized in the foregoing description, is a very irregular process, its result being the transformation of each chromosome into an irregular alveolar-reticulate structure showing nothing which can with any justice be called doubleness. After an inspection of the figures of longitudinal and cross sections of the telophase chromosomes (figs. 5–11) further argument on this point would seem to be superfluous. Secondly, the alveolar-reticulate bands into which the resting reticulum breaks down in early prophase, and which are probably in all cases continuous with the similar bands (chromosomes) of the preceding telophase, are not transformed directly into the split spirems of the later prophase, but give rise to single threads in which the definitive split is formed as the result of a process which appears to begin with the development of an axial series of new vacuoles. It has been shown that as these single threads are evolved most of the vacuoles and open spaces which had their origin in the preceding telophase, and which constitute the openings in the resting reticulum, become lost through the breaking down of their boundaries, so that the telophasic vacuoles, whether so situated as to make the chromosome double or not, take little or no part in the development of the definitive split.

It may here be questioned whether the vacuoles and open spaces which appear and split the thin prophasic thread may not be at least partly retentions from the preceding telophase, the split therefore being initiated in the telophase after all. This is a question which it has not been found possible to answer in many cases, since the changes in question occur in very minute structures which cannot be interpreted at all in any but the most favorable preparations. There can be no doubt, however, that the threads for considerable distances are actually single so far as the microscope will allow us to determine, and that many new vacuoles and open spaces develop where none were visible before. On the other hand it seems very probable that a few spaces of the earlier prophase, and hence of the preceding telophase, may occasionally persist in the heavier portions of the threads as they develop from the reticulate bands, such spaces if properly situated being incorporated in the later true split. But only in a very strained sense could such occasional vacuoles or spaces be said to constitute the initial stages of the split; their relation to it appears to be fortuitous rather than determinative.

It may also be questioned whether the single thread stage of the prophase, upon the importance of which the writer has insisted, is a phenomenon of general occurrence or is a special process peculiar to a few types of cells. To this question also no full answer can be given at present. It surely occurs in the root cells of Vicia and Tradescantia in spite of the fact that it does not appear in the descriptions given by other investigators of mitosis in these plants. It is also represented in Müller's (1911) figure 9 of *Najas marina*, and in the "spiral threads" figured by Bonnevie (1908, 1911, 1913) for Allium, Amphiuma, and Ascaris; by Wilson (1912) for certain insects; and by several other investigators. How much more widespread it may be cannot be stated, especially since the prophasic changes have been followed with sufficient care in so relatively few cases.

On the contrary, it is not impossible that in some forms the split spirem may develop directly from the alveolar-reticulate bands of the earlier prophase by a rearrangement of the vacuoles and openings to form a single median series as the structures become more slender, but the writer is not convinced that such a process has been demonstrated in any instance. Even if, for the sake of argument, it were assumed to occur, it would not necessarily follow that the telophasic vacuolation should be regarded as a splitting or that the chromosomes of the late telophase, resting stage, and early prophase should be regarded as double when the vacuoles and openings have such an arrangement as that described for Vicia and Tradescantia. Chromosomes in this condition are not double in any sense of the word, even though they contain open spaces which may later join with others to form a split. The chromosome can be said to be "double" or "split" only when its substance has been separated into two distinguishable portions, either by the rearrangement of the vacuoles and spaces as provisionally assumed, or, as is in all probability actually the case, by the formation of a median series of vacuoles and spaces which are for the most part if not entirely of prophasic origin. It may again be emphasized that in Tradescantia, as in Vicia, the alveolar-reticulate condition of the telophase and the early prophase does not pass directly into the split spirem stage as above provisionally assumed; but rather, by a peculiar process in which most if not all of the old vacuoles and openings are lost, the reticulate chromosome takes the form of a single thread in which the split then develops anew. In these forms the chromosome split, whether entirely new or partially built of vacuoles of earlier origin, cannot be regarded as anything but a prophasic development.

Method of chromosome splitting. Much interest centers about the exact manner in which the chromosomes undergo splitting because of its great importance in connection with current theories of the mechanism of heredity. The early view that the splitting of the chromosomes is primarily a division of a series of smaller units which it contains has been widely accepted, especially by those whose investigations have been concerned with the cytological aspects of the problem of inheritance. The hypothesis which postulates the existence of small units of inheritance, or genes, within the chromosomes has been of incalculable value in organizing the data of genetics, and new evidence constantly adds to the probability that such units are not purely conceptual ones. But it must be said that this evidence is genetical rather than cytological in nature. Although many cytologists have regarded the visible chromatin accumulations or granules as such units and have figured their division, others have found it increasingly difficult to see in these chromomeres anything significant in this connection. For the most part they seem to be quite inconstant in number and disappointingly irregular in behavior.

In the somatic cells of Tradescantia, as in Vicia, chromosome splitting seems to be initiated by a series of axial vacuoles which quickly develop into openings through the homogeneous chromatin thread, and not by the division of chromatic granules supported by the thread. As the openings become more numerous the chromosome takes the form of a ladder, the rounds being represented by the material between the successive openings (fig. 21). As the rounds or cross pieces gradually become thinner and finally break at the middle, thus completing the split, their material accumulates in two small lumps opposite each other in the two halves of the chromosome. The "paired granules" or "divided granules" described by many workers are without doubt to be explained in this manner. Such being their mode of origin, it is difficult to assign to them the rank of morphological units, or to attribute to them any specialized function in the hereditary process. In the microsporocytes of Vicia, however, the writer has observed chromatic granules of a much more definite character, but is not prepared to make any statement with regard to their significance.

The view that such granules do have some special significance is strongly favored by Wenrich's (1916) striking observations on Phrynotettix. Not only do the granules or chromomeres of a given member of the chromosome group in this form have relatively constant sizes and positions, but they also show close correspondence in the two members of a conjugating homologous pair. This is precisely the type of chromosome organization called for by our most promising theory of the cytological mechanism of heredity, which it is hoped will find further verification in additional observations as carefully made as those of Wenrich.

Bearing on problem of chromosome reduction. As stated in the introduction, the theory of telophasic splitting has been incorporated in an interpretation placed upon the reduction phenomena by Fraser (1914), Digby (1914, 1919), Nothnagel (1916), and certain other writers. The split seen in the early heterotypic prophase is said to have its origin in the telophase of the last premeiotic division, each chromosome persisting through the intervening resting stage in the double condition. It is consequently held, as fully stated by Digby (1919) in her account of the archesporial and meiotic phases in Osmunda, that the lateral pairing of slender threads in the heterotypic prophase, which a large school of cytologists has regarded as a conjugation of entire chromosomes, is in reality only the reassociation of the two halves of one chromosome which has been split in the preceding telophase. Such a reassociation is thought to occur in every prophase, somatic and meiotic, since these workers regard chromosome splitting as universally a telophasic phenomenon. The split thus thought to form in the premeiotic telophase functions in the homoeotypic mitosis; the latter mitosis is therefore looked upon as a continuation of the premeiotic division, the heterotypic mitosis being an interpolated process bringing about reduction. Not only does this premeiotic split reappear in the anaphase of the heterotypic mitosis to function in the homoeotypic, but a new split developing in the heterotypic telophase, after being temporarily obscured, functions in the post-homoeotypic division.

As the writer (1920) has pointed out in a review of Digby's contribution, the above outlined theory of reduction has certain advantages, for "it allows one interpretation to be placed upon the double spirem in both somatic and heteroptyic prophases, . . . and it also helps to explain the sudden appearance of the split for the second maturation mitosis in the anaphase of the first."

But can it be said that the chromosomes undergo splitting in the last premeiotic telophase and remain double through the ensuing resting stage? The writer believes that it has been shown in the case of ordinary somatic mitosis in Vicia and Tradescantia that the telophasic alveolation is in no sense a split. This conclusion rests upon the facts brought out in a detailed analysis of the telophasic changes themselves, and upon the fact that the early prophasic reticulate condition, which all grant is continuous with that of the preceding telophase, does not pass directly into the double spirems, but gives rise to single threads in which a new split develops, entirely or mainly by a new vacuolation, making the threads really double for the first time. This being true, it follows that the chromosomes at the beginning of the heterotypic prophase are *single* (although alveolar-reticulate), unless, indeed, the premeiotic telophase differs fundamentally from other somatic telophases, which is not supposed to be the case. Consequently, if it is argued that the doubleness of the spirem in the heterotypic prophase is due to a splitting and not to a conjugation, it must be done upon other grounds; the principle of the telophasic split is evidently a false premise.

From the above considerations it appears that chromosome behavior during the somatic telophase, instead of giving the key to the reduction process, shows rather that the solution of this perplexing problem must be reached mainly through a more refined analysis of those changes in the heterotypic prophase itself which have led so many observers to conclude that the association of chromatic threads at that stage represents the conjugation of entire chromosomes which separate at the first maturation mitosis.

SUMMARY

The principal results of the present study of Tradescantia may be summarized as follows:

1. During telophase the chromosomes become transformed by a process of irregular vacuolation into alveolar-reticulate structures which together make up the resting reticulum. In rapidly multiplying cells the visible limits of the constituent chromosomes may not be entirely lost between successive mitoses.

2. In prophase the constituent reticulate chromosomes separate from one another through the breaking down of their connecting anastomoses; each gives rise to a single slender chromatic thread in which the definitive split develops as a new formation, though old vacuoles may occasionally be incorporated in it.

3. The telophasic vacuolation cannot be interpreted as a splitting of the chromosomes; the chromosomes are therefore not double during the resting stages. The splitting of the chromosomes is a phenomenon of the prophase.

4. No direct evidence has been found favoring the view that the splitting of the chromosomes is primarily a division of smaller chromatic units or chromomeres.

5. Interpretations of the phenomena of the heterotypic prophase are unsound in so far as they rest upon the assumption of telophasic splitting in somatic cells.

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EXPLANATION OF PLATES

PLATE XXII

All figures except no. 8 were drawn at the level of the table with the aid of an Abbé camera lucida under a Zeiss apochromatic objective, 2 mm. N.A. 1.40, with compensating ocular 18. They have been reduced one-half in reproduction and now show a magnification of 1900 diameters. Fig. 8, × 950.

FIG. 1. Metaphase: chromosomes attached to spindle by middle points.

FIG. 2. Anaphase: daughter chromosomes separating.

FIG. 3. Later stage: daughter chromosomes passing to poles.

FIG. 4. Late anaphase: chromosomes massing at poles.

FIG. 5. Telophase: vacuoles appearing within chromosomes; anastomoses present.

FIG. 6. Slightly later stage; note arrangement of vacuoles.

FIG. 7. Two telophase chromosomes, showing irregularity of vacuolation.

FIG. 8. Telophase, showing polarized arrangement of chromosomes (camera lucida sketch).

FIG. 9. Cross sections of telophase chromosomes, showing the same.

FIG. 10. Later telophase: nucleus larger and nucleoli present.

FIG. 11. Late telophase: limits of chromosomes still visible.

FIG. 12. Interphase or resting stage.

PLATE XXIII

FIG. 13. Resting stage in which telophasic changes have gone further.

FIG. 14. Early prophase: reticulum breaking up into constituent chromosomes.

FIG. 15. Later stage: chromosomes further separated and more condensed.

FIG. 16. Cross sections of chromosomes like those of figure 15.

FIG. 17. Prophase nucleus with most of its chromosomes in single thread stage.

FIG. 18. Chromosomes in single thread stage; development of this condition from reticulate stage shown at *a*.

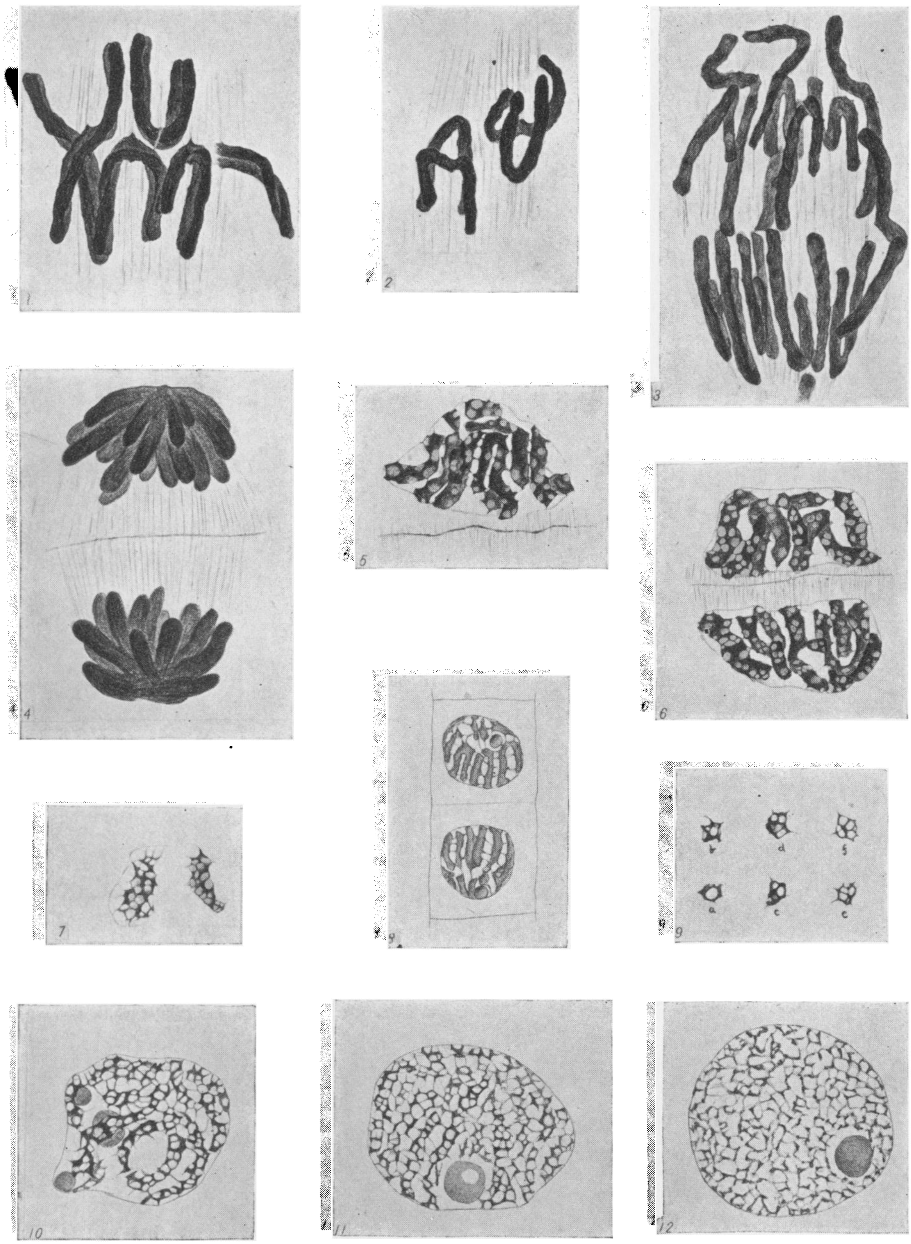
FIG. 19. Splitting of single threads.

FIGS. 20, 21. Later stages: vacuoles and openings more numerous; chromosomes thicker.

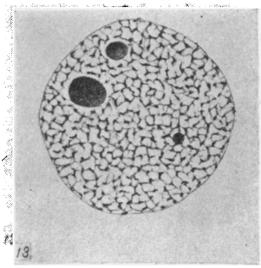
FIG. 22. Prophase nucleus with some chromosomes partially and some completely split.

FIG. 23. Later stage: chromosomes heavier but not completely split.

FIG. 24. Late prophase: chromosomes swollen and split obscured; nuclear membrane has disappeared and spindle is developing.



SHARP: SOMATIC CHROMOSOMES IN TRADESCANTIA.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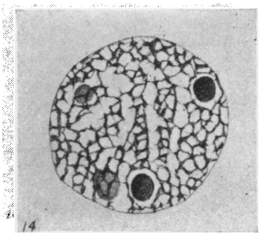
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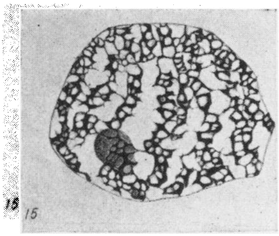
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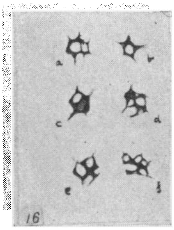

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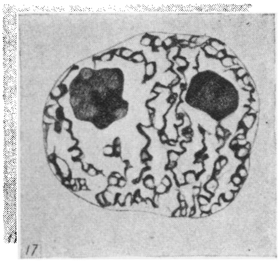
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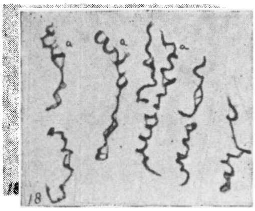

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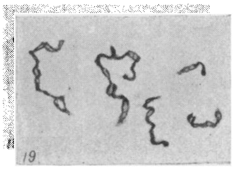
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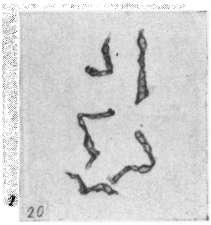
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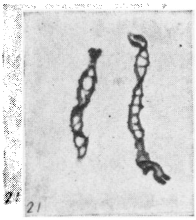
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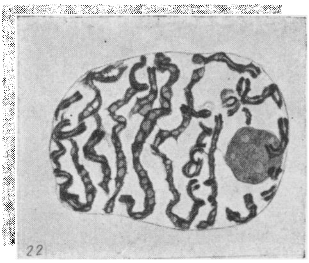
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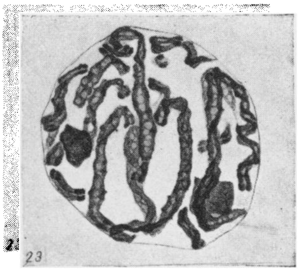
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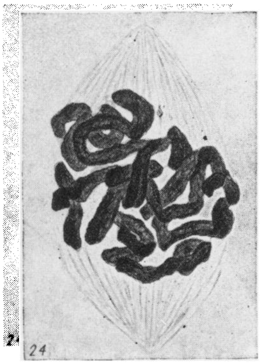
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SHARP: SOMATIC CHROMOSOMES IN TRADESCANTIA.